

Inside Evolution: 1992 Presidential Address

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Abstract

The relationship between an organism's life history, its ontogeny, and its evolutionary history fascinated biologists during much of the nineteenth century. However, with the shift in emphasis away from embryology to natural selection in the latter part of the century, the study of this relationship between ontogeny and phylogeny drifted into the backwaters of evolutionary theory. The last 15 years has seen a resurgence of interest in this topic. Recent studies have revealed that this relationship, known as heterochrony, plays a pivotal role in evolution, forming the link between genetics and natural selection. Heterochrony can be invoked to explain much intraspecific phenotypic variation, including polymorphism and sexual dimorphism. Many interspecific examples of heterochrony demonstrate that dissociation is a common phenomenon, with some features being paedomorphic (ancestral juvenile characters present in the adult), while others are peramorphic (ancestral adult characters present in the juvenile). Selection of heterochronic morphotypes is shown to focus sometimes on factors other than morphology. For instance, size or life history strategy might also be targeted. Extrinsic factors, such as predation pressure, are considered to play an important role in directing evolutionary trends that have been facilitated by heterochrony.

Introduction

A golden thread runs through the history of life. It is a thread that links sea urchins to apple maggot flies, snails to lungfishes, delphiniums to emus, and salamanders to humans. This connecting thread is the sequence of changes that occur to individual as it develops from embryonic to adult form. The importance of such changes was recognised by the ancient Greeks. Aristotle, for instance, believed that a sequence of increasingly more "complex" souls—nutritive, sensitive, then rational—entered the human embryo during its growth and development. What Aristotle and his contemporaries were recognising was the enormous and profound morphological changes that the human embryo, like the embryos of most other organisms, undergoes during early growth.

During the early part of the nineteenth century embryological studies dominated biological thought (Gould 1977). The great embryologist Karl Ernst von Baer recognised that similarities between animal's early developmental stages indicated an evolutionary relationship between such forms. While von Baer argued that it was invalid to compare directly the adult form of one animal with the juvenile stage of another, the realisation by some early 19th century palaeontologists that some sequences of fossils appeared to be arranged in a sequence comparable with embryonic changes led to the formulation of one of the great biological "laws" of the 19th century: the Law of Recapitulation.

Palaeontologists such as Louis Agassiz, who worked on fossil fishes in Switzerland in the 1830s and 1840s, argued, for example, that the form of the tail in adult fishes observed in the fossil record paralleled the development of the tail in modern fishes, from early embryonic stages to the adult stage. Thus the developmental stages of living teleosts often show that small juveniles have a simple tail, later juveniles a so called heterocercal tail, and final

juvenile a homocercal tail where top and bottom fins are the same size. This parallels the perceived evolutionary sequence (see McKinney & McNamara 1991, Fig 1-1).

But the one scientist to really promote this concept was Ernst Haeckel in the 1860's. In his most influential tome *Generelle Morphologie der Organismen*, Haeckel proposed his famous "Biogenetic Law" that was to become known to many future generations of biology students as "ontogeny recapitulates phylogeny"; an organism's developmental history, from fertilization to adulthood, contained within it the whole history of the evolution of that particular group. The argument was that our early embryos pass through stages that resemble, at one time worms, at another fishes, at another reptiles, before passing into a "mammalian" stage. The influence of Haeckel's work was profound. Many later 19th century biologists based the classification of whatever group they were studying in terms of the Biogenetic Law. It led some palaeontologists, such as Alpheus Hyatt, to select his ammonites and arrange them in evolutionary sequences to fit in with the Biogenetic Law, ignoring the stratigraphical data which showed no correspondence whatsoever.

But why did this powerful influence on biological thought for much of the 19th century seemingly just fade away into oblivion? Were Haeckel and his colleagues completely wrong? Is there no relationship between ontogeny and evolution? Or is the relationship different from that which the Haeckelian school perceived?

The demise of the relationship between ontogeny and evolution can be attributed to a number of factors. One was the publication in 1859 of Charles Darwin's 'Origin of Species', a book that shook the very foundations of both biology and theology. Most previous attempts to unravel the mysteries of the origins of species had been inward looking. They had concentrated on relationships intrinsic to the organism; to what was going on inside the organism as it developed. Darwin, on the other hand, changed the focus and looked at the extrinsic factors that affected why

particular species survived and others didn't: the role of competition; of the struggle between individuals; of the effect of the environment on selecting species.

Combined with this was the increasing number of examples in the fossil record where ontogeny didn't seem to be recapitulating phylogeny; it seemed that phylogeny was reversing ontogeny, with later forms resembling juveniles of their ancestors. But it took until the 1920's for someone to actually articulate what really appeared to be going on. That person was the marine biologist Walter Garstang, who studied tunicates (sea squirts), in particular their larvae. He argued (Garstang 1928) that vertebrates could have evolved from something as inconsequential as the larva of a sea squirt. This larva possesses all the attributes that one would expect in a vertebrate: a notochord; a dorsal hollow nerve chord; gill slits and a postanal propulsive tail. Garstang called this phenomenon of the retention of ancestral juvenile characters *paedomorphosis*—literally 'child shape'. He observed the same character in other groups of animals. For instance he noticed that there existed a number of salamanders that bred in water, and never metamorphosed into a terrestrial adult and retained a number of juvenile characters throughout their life. This is the poem that Garstang wrote, as he can describe it much more elegantly than I:

The Axolotl and the Ammocoete

*Amblystoma's a giant newt who rears in swampy waters,
As other newts are wont to do, a lot of fishy daughters:*

*These Axolotls, having gills, pursue a life aquatic,
But, when they should transform to newts, are naughty and
erratic.*

*They change upon compulsion, if the water grows too foul,
For then they have to use their lungs, and go ashore to prowl:
But when a lake's attractive, nicely aired, and full of food,
They cling to youth perpetual, and rear a tadpole brood.*

*And newts Perennibranchiate have gone from bad to worse:
They think aquatic life is bliss, terrestrial a curse.*

*They do not even contemplate a change to suit the weather,
But live as tadpoles, breed as tadpoles, tadpoles altogether!*

Garstang effectively turned the Biogenetic Law upside down. However, this did not herald an upsurge in interest in the role of development in evolution. On the contrary. Few biologists had little faith left in the ability of the developmental history of an organism to tell us much about its evolutionary history. Two other factors combined to relegate such studies to the backwaters of biology. Firstly, there was the emergence of the study of genetics from the 1930s onwards. Second, was the most horrendous terminology ever perpetrated on mankind that arose from ontogenetic studies. Terms existed such as *paedomorphosis*, *peramorphosis*, *paedogenesis*, *progenesis*, *proterogenesis*, *palingenesis*, *pangeneses*, plus many more.

Fifteen years ago the American palaeontologist Stephen J. Gould published a book called 'Ontogeny and Phylogeny' in which he investigated the role of recapitulation and *paedomorphosis* in evolutionary theory. This book marked a renaissance in studies of the relationship between ontogeny and evolution, for what Gould (1977) argued was very simple. Haeckel and Garstang were both wrong, and they were both right. Recapitulation, in a very general sense, and *paedomorphosis* are both valid mechanisms for the generation of new morphologies. My own studies started in the 1970s at the time that Gould was writing his book, and our work, together with that of an increasing number of biologists and palaeontologists around the world has revealed that rather than being just a quaint evolutionary phenomenon, the study of the role of ontogeny in evolution is one of the cornerstones of evolution.

Indeed, it can be argued that it is the missing link in evolutionary studies. It is the link between genetics at one extreme and natural selection at the other, for it is the subtle changes in the rate and timing of development over countless generations that provides the raw materials on which natural selection can work.

In this address I propose to demonstrate countless examples of this phenomenon, to illustrate not only how it fits into current evolutionary theory, but also how it can explain the great diversity of life forms that exist on Earth today, and have existed since life evolved on this planet some 3.5 billion years ago. Without such changes to the rate and timing of development, life would not have evolved on this planet the way that it has.

Evolution means change—we think of it as the evolution of one species from another, or of one population of individuals from one another. Most people, I suspect, when they think about how living things have evolved probably think of how humans evolved from the apes, or how the animals and plants with which they are familiar came into being—but always from the viewpoint of adult animals or mature plants. Just picture any of the illustrations that have been used to chart the stately progression of *Australopithecus* to early species of *Homo*, through to *Homo sapiens*. Inevitably such illustrations depict adults (usually males), evolving from one into the other. But if we focus on the individual organisms—think about yourself if you like—then each organism undergoes a phenomenal degree of change from its moment of conception until it dies. You might think that there has been a dramatic change in appearance from an 'ape man', such as *Australopithecus*, to modern man. But this is nothing when compared with the morphological changes that occur as an individual of a single species develops.

Although your cognisant memory doesn't in reality allow it, let your imagination take you back to the time before you were born—go back to the first few days of your existence following conception. Think about what you looked like a few weeks after conception, the relatively enormous head and tiny limbs. Then you will realise the remarkable changes that you have undergone to get you to what you have become today. This is your ontogeny—your growth and development from embryo through juvenile to adult.

Now just consider for a moment what would happen if the orderly rate and timing of development of your bodily parts had been altered. If the rate at which a feature that changed mostly during the latter part of your juvenile development was slightly altered you might end up with a slightly longer leg, or perhaps shorter arm than usual. However, if a critical feature that formed early in your embryonic development, such as a limb bud, had perhaps started its growth either a little earlier or a little later than normal, or even not at all, then the consequences for your adult shape would have been tremendous.

This whole concept of changes to the timing and rate of development is known as *heterochrony* (literally 'changing time'). Basically the 'amount' of growth than an organism goes through during its ontogeny can be more than its ancestor or it can be less (Fig 1). This can apply to the organism as a whole, or to specific structures, like an arm, a leg, or whatever. More growth is known as *peramorphosis* (literally, 'beyond growth'). Less growth is known as *paedomorphosis*, as I mentioned earlier. Each of these states can be achieved in three basic ways (Alberch *et al.* 1979; McNamara 1986). A structure can start growth later than in the ancestor, but finish at the same time. This is known as *postdisplacement*. Alternatively an organism, or a

HETEROCHRONY

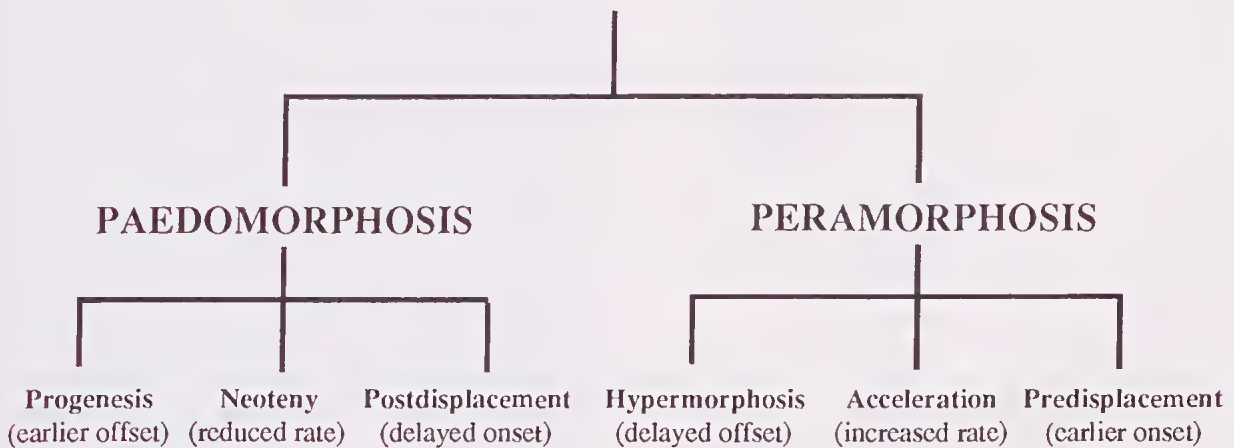


Figure 1. The hierarchical classification of heterochrony.

particular structure can grow at a slower rate than in the ancestor. This is known as *neoteny*. The last way to achieve paedomorphosis is for the organism, or part of the organism, to grow at the same rate as in the ancestor, but to finish growth earlier. This is known as *progenesis*.

The three ways to achieve *peramorphosis*, in other words, developing beyond the ancestor, are the opposite ways that paedomorphosis were achieved. Development can start earlier (*predisplacement*), and so get a head start; or it can go at a faster rate (*acceleration*), so developing further in the same time; or it can simply develop for a longer time and go farther (*hypermorphosis*), termination of growth being later than in the ancestor. These three pairs of mechanisms that target either the time of onset of development, its rate or its time of offset are the crux of heterochrony. And they can be used to explain much of the diversity of life.

Specific examples show how heterochrony operates within species; how it operates between species; how it can be affected by environmental factors; how it can be used in macroevolutionary studies to explain the evolution of major groups of organisms; how it demonstrates that natural selection may be targeting features other than an organism's morphology; how evolutionary trends can be explained; and illustrate how evolution affects the whole of an organism's life history.

Heterochrony within species

Let me take you gently into the world of heterochrony by introducing you to a character with which you are probably very familiar, but which you may not recognise at first—the early Snoopy. The cartoon character Charlie Brown's canine companion is immediately recognisable today as a dog that is largely all head, with diminutive limbs, and less than impressive body. But the very first Snoopy created some decades ago was quite different.

Here was a fairly typical, happy-go-lucky dog, long of limb and long of tooth and jaw, most unlike his evolved form we see in newspapers and comic books today. Now, consider how this prototype Snoopy changed as it grew from a cute, cuddly little puppy into a bundle of canine energy. The changes in shape that an average dog goes through from birth to adulthood are quite profound (see Wayne 1986). Apart from an increase in size, many of the

body proportions change quite appreciably. For instance the legs become relatively longer and the skull undergoes a great elongation, changing from a near-rounded shape in early juveniles, to a long muzzled shape in adults. Now, just imagine what would happen to our prototype Snoopy if it became sexually mature much earlier than its immediate ancestor, resulting in the premature cessation of growth. What would our dog look like? He would look like the Snoopy as we know him today—a paedomorphic dog.

While here we are dealing with what might be a subconscious desire on the part of the cartoonist to select for 'cuteness' (see Gould's [1979] similar analysis of the evolution of Mickey Mouse), a character that is of selective advantage to a juvenile dog, this is more than just a mere flippant example of the concept of heterochrony. Let us consider heterochrony in real dogs. The many and varied breeds of the domestic dog differ from each other largely in terms of body size and growth rate. Some, such as chihuahuas or King Charles spaniels, differ from an average dog by retaining, as adults, ancestral juvenile characters—they are paedomorphic in retaining a much smaller muzzle and a relatively large cranium. An Irish Wolfhound, on the other hand, is peramorphic, having gone "beyond" the ancestral dog in its degree of development, attaining a greatly prolonged muzzle (Fig 2). These major differences in the appearance of these breeds have an underlying genetic basis in the control of the rate and timing of production of growth hormones.

The underlying importance of this great change in growth proportions during ontogeny is shown by comparing the growth of a dog skull with that of a cat. In terms of overall body shape and proportions, dog breeds exhibit a far greater range than do breeds of cat (Wayne 1986). This arises from the much higher proportionate growth rate of the dog skull, particularly with regard to the length of the muzzle (Fig 3A,B). In cats, on the other hand, there are much lower proportionate growth changes (Fig 3C,D). There is thus a smaller range of variations to be selected from in cats, compared with dogs.

Environmental effects can act directly on certain members of a population to produce unusual growth forms by heterochrony. One such example is the effect that diet has on growth in the caterpillar *Pseudoloaletia unipuncta*. Experiments of Berneys (1986) have shown that the proportionate size of the head can change, depending on the nature of the

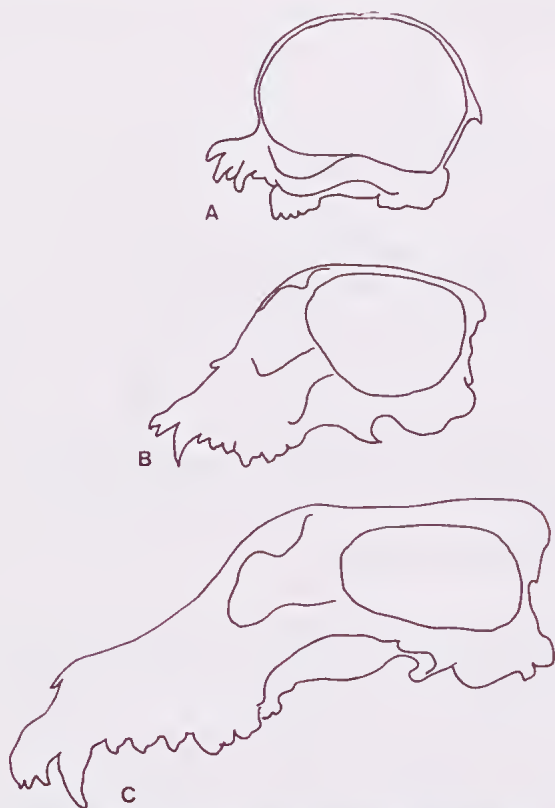


Figure 2. Transverse sagittal sections through skulls of adult dogs: A, King Charles spaniel; B, English bulldog; C, Irish Wolfhound. Compared with the bulldog, the spaniel is paedomorphic, and the wolfhound peramorphic. Redrawn from Weidenreich (1941).

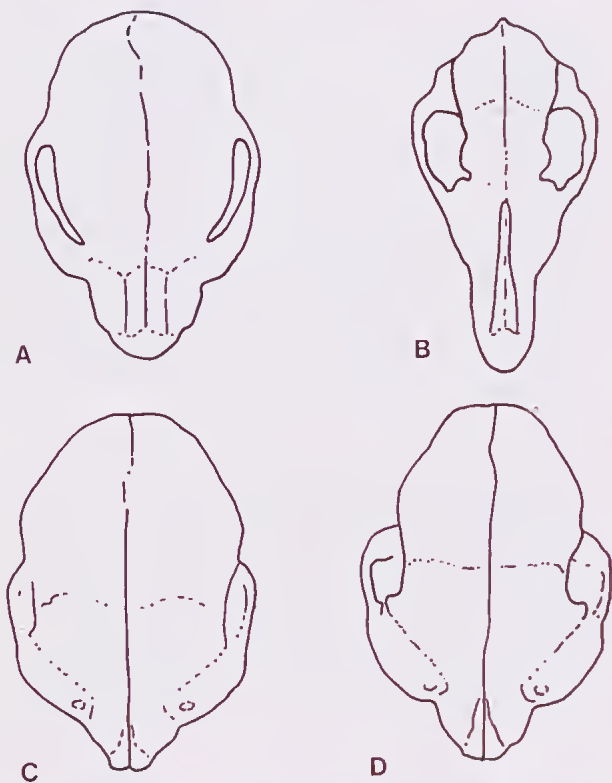


Figure 3. Dorsal view of skull of juvenile domestic dog (A) and adult dog (B), contrasted to that of juvenile domestic cat (C) and adult cat (D). Note the greater degree of morphological change during ontogeny of the dog skull compared with that of the cat. Skulls are normalised for size. Redrawn from Wayne (1986).

diet. Caterpillars fed on a diet of grass develop heads twice the mass of those fed a soft artificial diet. Those fed an intermediate diet developed an intermediate head size. These differences in overall head size have been attributed to increased muscular development. There is a genetic basis to these changes, for of 82 species of grasshoppers and 76 species of caterpillars from North America and Australia, grass eaters consistently have larger heads than herbaceous plant eaters. Here is an example of peramorphosis acting not on the whole organism but on one particular structure. I shall discuss later this "dissociation of parts".

Environmental factors such as temperature can also have a profound effect on what an organism looks like. This is well shown in some molluscs. For example, the Atlantic squid *Sthenoteuthis pteropus* occurs as three polymorphs: a small form, a medium form and a large form (Zuev *et al.* 1979). There is a direct correlation between maximum size reached and time of onset of maturity. There is also an inverse correlation between higher temperature and increasing size. Consequently the smallest forms of this squid occur in oceans with a water temperature between 26-30°C; large forms in water between 18-22°C (McKinney & McNamara 1991, Fig 4-4). The same phenomenon is exhibited by the Indo-Pacific squid *Sthenoteuthis oyalmiensis*; early and later maturing males and females differ in final body size, the earlier maturing forms being restricted to warmer water. So, these forms can be considered as paedomorphic early finishers, or progenetic forms (Fig 1).

One of the classic examples of paedomorphosis occurs in the salamander known as an axolotl, or Mexican salamander. These salamanders' rate of morphological change is so reduced that it fails to metamorphose and so retains its larval gills, even when sexually mature. It also retains ancestral juvenile behavioural patterns by remaining in the juvenile aquatic environment and not metamorphosing into a land-dwelling form.

Such paedomorphosis is common in salamanders (Sprules 1974; Larson 1980; Alberch & Alberch 1981). Many different lineages show similar changes in morphology. In descendant species the tails become shorter, feet become fully webbed and the skulls are less bony, features of adult paedomorphic salamanders that occur in juveniles of their ancestors. Many of these paedomorphic species have a slower growth rate (neoteny). However, some finish development earlier (progenesis). So here we can see that paedomorphosis in one group of animals can be achieved by two quite different mechanisms.

One intriguing question is why some populations of salamanders include paedomorphic individuals while others do not. Harris (1987) investigated this by raising larvae of the salamander *Notophthalmus viridescens dorsalis* in tanks under different population densities. Those kept at low population densities (10/tank) became paedomorphic and stayed in the water and bred in a juvenile form, while those at high population density (40/tank) metamorphosed into immature land-dwelling salamanders. This seems to make evolutionary sense. In the wild as ponds dry up, so the population density would increase. Under such circumstances selection would favour those individuals that metamorphose into terrestrial salamanders and disperse.

But why should some groups of animals, such as salamanders, show such a common occurrence of paedomorphosis both today and in the fossil record? Theoretically there is no reason why paedomorphosis should occur any more often than peramorphosis. Perhaps the answer to the high frequency of paedomorphic salamanders lies in the size of their cells. The larger the cell, the more DNA it is

likely to hold. The amount of DNA in a cell is known as the 'genome size' or 'C-value'. It would seem that there is a negative correlation between genome size and developmental rate. Many salamanders have high C-values. Sessions and Larson (1987) analysed the C-value for 27 species of amphibians and found that those with larger cell volumes had a slower developmental rate than those with smaller cell volumes.

A similar situation is found in lungfishes, with modern day species having large C-values. It is known from morphological studies that modern species are paedomorphic when compared with their ancestors (Bemis 1984), which have a good fossil record dating back more than 350 million years in to the Devonian. By analysing the size of bone cells over this period it can be demonstrated that there has been a general increase in cell size (Thomson 1972), corresponding to the paedomorphic morphological changes that have been documented.

Heterochrony can produce not only shape but also size changes. Shorten the period of juvenile growth of an organism (progenesis) and it will not grow as large as its ancestor. Conversely, lengthen the growth period (hyper-morphosis) and the organism will grow larger. Many species, such as some ants, possess polymorphs of different sizes. Likewise many species exhibit sexual dimorphism. This, more often than not, is manifested in differences in size between males and females. Such differences are often caused by variations between polymorphs, or between sexual dimorphs, in the timing of cessation of growth i.e. differences in the timing of onset of sexual maturity.

Arguably the most extreme form of sexual dimorphism, and one that vividly illustrates the difference in degree of morphological development between sexes, occurs in an obscure group of gastropods, known as eulimids. In these genera such as *Entocolax*, *Entoconcha*, *Thyonicola* and *Enteroxenos*, the females live as parasites within holothurians, otherwise known as sea cucumbers. For many years it was thought that many of these species were hermaphrodites, until it was realised that what had been interpreted as the testes was in fact the entire male animal (Lützen 1968). The male lives within the female, entering her through the ciliated tubule that connects the female to its host's esophagus. The minute male attaches itself to a special receptacle within the female's body, where it grows into what is essentially little more than a testis (Fig 4). Such dimorphism, with a smaller paedomorphic male living within or upon the female, is not uncommon in invertebrates, particularly among molluscs and echinoderms.

Although similar extreme examples are not common in vertebrates they do occur. Perhaps the best known is the deep-sea angler fish *Photocorynus*. In this fish the male is very much smaller than the female and lives parasitically attached to the female's head. While the female reaches lengths of about one metre, the male is rarely longer than 15 cm. A recently described example (Hutchins 1992) is almost as stunning. The females of some species of leatherjackets much more closely resemble the juveniles in body shape than the males because the males have undergone a greater degree of ontogenetic change. Whether this is because males mature later than the females or whether they have accelerated growth is not known. There are also substantial differences in the skeleton between the male and female, again the female resembling the juvenile. Hutchins considers that a consequence of the difference in fin shape between the male and female explains differences between the two in the way that they swim. Developmental changes can induce behavioural differences too.

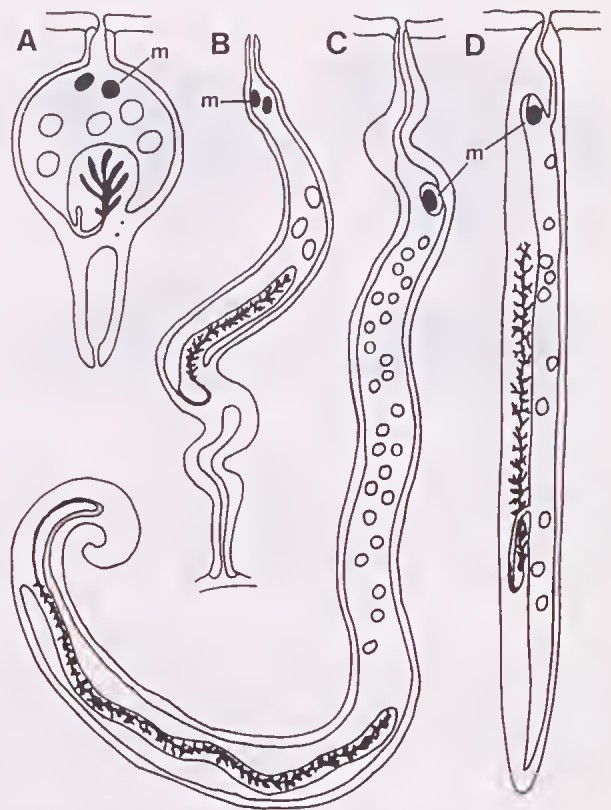


Figure 4. Extreme sexual dimorphism in eulimid gastropods, endoparasitic in holothurians. The progenetic male (m) lives within the female. A, *Entocolax*; B, *Entoconcha*; C, *Thyonicola*; D, *Enteroxenos*. Redrawn from Lützen (1968).

Heterochrony between species

The vast majority of differences between species in all groups of organisms are caused by changes to the timing and rate of development. We can try applying some of the principles of heterochrony to one of the classic examples of evolution—Darwin's Galapagos finches (Fig 5). Hitherto this classic example of evolution has been looked at purely from a natural selection point of view. I would like to look at it from the inside—from the point of view of structural changes that have taken place in the evolution of particular species to allow the adaptation to differing feeding habits.

The Galapagos finches show a wide variation in bill shape. These have allowed a wide range of food types to be utilised. Some bills are used for crushing, mainly different types of seeds; others are for probing; others for grasping and biting, predominantly insects. Such adaptations are often interpreted as having evolved "in order for the species to feed on a particular object", as though natural variation would only allow a particular bill shape to evolve if the necessary food was available. This "cart before the horse" approach ignores the role of heterochrony in the evolution of these bills. Because of these subtle changes to the growth rates of upper and lower beaks a wide range of morphotypes has evolved. Thus upper beaks that have increased their relative growth rate did so by peramorphosis, whereas those that underwent reduced growth rate are paedomorphic. This combination of heterochronic styles is known as dissociated heterochrony. Only if suitable food sources were available which could be exploited by a particular bill shape would this shape be selected for. The source of variation behind such evolutionary radiations is



Figure 5. Heads of four species of Galapagos finches, showing variation in bill shape and size. 1. *Geospiza magnirostris*; 2. *Geospiza fortis*; 3. *Geospiza parvula*; 4. *Certhidea olivacea*. Reproduced from Darwin (1839).

heterochrony arising from internal factors, rather than the external pressure of natural selection. This does not argue against natural selection. Two factors must operate in tandem; evolution is the product of both intrinsic and extrinsic factors.

Dissociated heterochrony can also be used to explain the macroevolution of some groups of birds. In particular the ratites, or flightless birds, such as the emu, ostrich, rhea and the extinct moa and aepyornis. De Beer (1956) claimed that flightless birds such as these were classic examples of the power of paedomorphosis to give rise to whole, new groups of animals. He argued that the very reduced wings and poorly developed breast bone showed that the ratites were paedomorphic birds. While not denying that these features are paedomorphic, I would argue that the characters selected for in ratites were not the the paedomorphic features, but two other features: the large body size, combined with the peramorphic legs. These, after all, are two important features of the ratites, without which they would not survive.

There is no doubt that ground dwelling birds are highly susceptible to predation. Just consider the fate of the dodo on Mauritius, the moa on New Zealand and the aepyornis on Madagascar. The reason for the possession of some paedomorphic features by these birds is that they were a necessary consequence of the selection for the peramorphic features. One was a trade off against the other. Just imagine what size wings an ostrich would require to get off the ground. Early Tertiary flightless birds, which were in fact the first large predators to exploit the niches vacated by dinosaurs, evolved enormous, powerful heads by peramorphosis. But they too would have evolved from flying birds and have also suffered paedomorphic reduction in wing size.

Probably the most important message to emerge from heterochronic studies in the last decade is the fact that not only do both paedomorphosis and peramorphosis occur but that most organisms are a product of these two opposing forces. And if you consider the number of morphological features in an organism that can have their growth trajectories altered, you will quickly realise that the potential combinations that can evolve is mathematically enormous. While many of these combinations would probably not be functionally possible, the diversity of life on this planet is testimony to the power of heterochrony to generate a sufficient diversity of successful forms.

Although there has been much less research on the role of heterochrony in plants, what has been done is showing that heterochrony operates equally well in plants (Guerrant 1988). From an Australian perspective Carpenter (1991) has stressed the importance of heterochrony in the evolution of the cycad *Macrozamia*, while recent work by Wiltshire *et al.* (1991) on some species of *Eucalyptus* has demonstrated the importance of paedomorphosis in leaf and fruit development.

Dissociated heterochrony figures as prominently in plants as it does in animals. Take for example the *Delphinium*. A study by Guerrant (1982) focused on *Delphinium nudicaule*, a species which is pollinated by hummingbirds. The external appearance of the flowers results from a reduced rate of development of the floral parts, producing a paedomorphic morphology. For example, the sepals face forward, as they do in the bud. This produces a tubular flower characteristic of plants pollinated by hummingbirds. Not all of the plant's features are paedomorphic, however. The petals, unlike the sepals, develop faster, which results in a shape beyond that of the generalised delphinium. So selection acting on the development of the flower in different ways, retarding some features, accelerating others, produced a new shape capable of attracting and rewarding a new pollinator. This was a major adaptive breakthrough for the plant, that didn't involve dramatic genetic changes.

Heterochrony and selection for body size

Many examples show selection acts on the shape of particular structures, but selection may be acting on other aspects of developmental change. There is one particular mechanism that either extends the period of growth or reduces the period of growth. The two resultant effects, progenesis for reduced growth, and hypermorphosis for extended growth, produce not only shape changes but also size changes. Reducing the juvenile phase of growth results in the evolution of a smaller adult body size than possessed by the ancestor; extending the growth period produces a larger adult.

The fossil record demonstrates many examples of evolutionary trends of increased body size (McKinney 1990). Such trends are so common that they have been codified as Cope's law. Heterochrony has been used to explain some of these size increases, for instance in titanotheres (McKinney & Schoch 1985) and the Irish Elk (Gould 1974; Fig 6). Here I will demonstrate this with two examples, one of which is also a classic evolutionary example—the evolution of horses. Recent analysis of the evolution of horses shows that rather than being a simple evolutionary trend leading from small browsing forms in the early Tertiary to larger grazers in the later Tertiary, there was a great complex of forms, which show an overall trend towards selection for larger body size (MacFadden 1986). Traditionally, the evolution of horses has been shown to be dominated by changes to the form of the foot, with an overall, paedomorphic reduction in the number of toes, and a change in the shape of the teeth that allowed a change from a browsing to a grazing habit. Many of the changes may be considered to be, in part, by-products of the selection for increased body size. Thus delay in onset of maturity will have allowed a larger body size to be attained, and this in turn will have dragged along proportionate changes in certain structures, such as the form of the teeth and legs.



Figure 6. The Irish Elk, *Megaloceros giganteus*. Although not confined to Ireland, nor an elk, this deer has been cited (e.g. Gould 1974) as a classic example of hypermorphosis, the large antlers being interpreted as a by-product of selection for large body size.

Another example is in dinosaurs. Early triceratopsians were small creatures, not the lumbering hulks that existed in the late Cretaceous. As a consequence, structures such as the large horns present on the head found in later large forms, were barely developed in early small forms (Fig 7). Selection for a larger body size resulted in structures such as these being also developed. The question to answer when attempting to interpret such trends is which factor was under strongest selection pressure: body size, or specific morphological features, such as the horns? It may have been that in the triceratopsians, even though primary selection was on body size, perhaps as a means of combating predation pressure, there was added benefit in that extension of the growth period allowed structures such as the horns to increase greatly in relative size.

Evolution is not always towards increasing complexity and larger size. Many small species of animals and plants are likely to have evolved from larger ancestors by heterochronic mechanisms, such as precocious onset of maturity (progenesis). For example, many small species of trilobites in the fossil record are thought to have evolved in this way (McNamara 1983). Although adults, they retain ancestral juvenile features, such as fewer body segments, and a small body size (Fig 8). The question that again must be asked is, what was selection acting upon: was it the particular morphological features attendant on the small size? Was it the small size itself? Or was it some other factor, and both shape changes and body size changes were a by-product of selection for some other factor?

Heterochrony and the selection of life history strategies

Classic life history strategy studies identify a continuum between forms that inhabit unstable environments where selection favours small forms, with short life spans, reproduce frequently and have large numbers of offspring (sometimes known as *r*-selected forms), and forms that inhabit stable environments, and have large body size, long

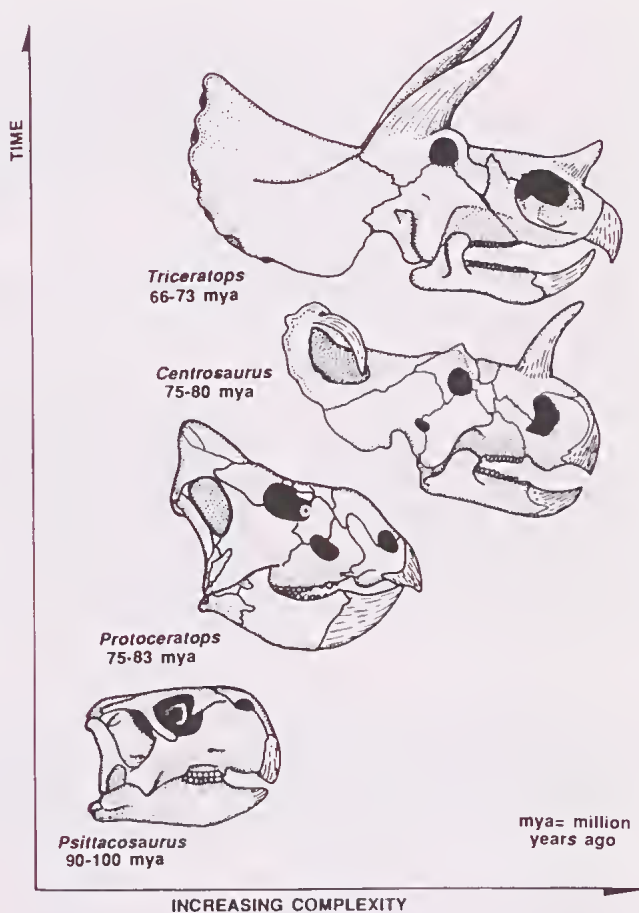


Figure 7. Evolution of the skull of triceratopsian dinosaurs, showing that as they increased in size, so horns and bone frills became more ornate. Later species are much larger than earlier species. Reproduced, with permission, from Long (1992).

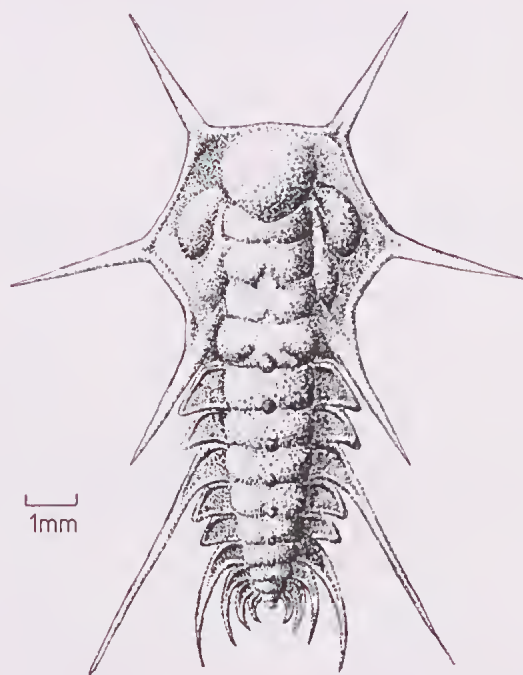


Figure 8. *Olenelloides armatus*, a progenetic trilobite from the early Cambrian of Scotland. Reproduced, with permission, from McNamara (1978).

life spans and reproduce infrequently with small numbers of offspring (sometimes known as *K*-selected forms). Let us consider some of these features of the two extreme forms. The small body size and short life span of those living in unstable, ephemeral environments corresponds to our "early finishers" or progenetic forms, that I have discussed earlier. The large body size and long life span of the other extreme are characteristic of the "late finishers", or hyper-morphic forms.

Hafner and Hafner (1988) have looked at heterochrony in some species of kangaroo mouse and kangaroo rats from North America in terms of life history strategies and have presented a very elegant model that shows how selection did not favour the length of the mouse's tail or the colour of its fur, or the size of its eyes, but the actual life history strategy of the animal. The morphological features that evolved were certainly not maladaptive to the animals, and must have also been of some adaptive significance. But the fact that one species might have a slightly longer tail than another shouldn't be explained in terms of what adaptive advantage this conferred to the species. It would merely have been a by-product of selection for some particular life style.

It had long been argued that the possession by these heteromyid rodents of features such as enormous head, huge hind feet, large eyes and long tail were all specific adaptations to living in a desert. The argument went that the large head counterbalanced the rodent as it hopped purposively through the cool desert night on its huge sand-paddle feet, searching for food with its big eyes and steering with its rudder-like tail. Not so, argue the Hafners. The small size and retention of ancestral juvenile traits by the adult kangaroo mouse *Microdipodops* is likely to have arisen because of early onset of maturity producing a mouse with a body length less than 8 cm. The adult of the larger kangaroo rat, *Dipodomys*, has similar ancestral juvenile characters, but these evolved by a reduction in the rate of development. This rat is much larger than the kangaroo mouse, with a body up to 20cm long. It has a longer life span, slower development, longer gestation period and smaller litters than the mouse. These are the features that were being selected for—not the fact that it might have had a few more whiskers, or slightly longer tail.

Another related rodent is a large pocket gopher that grows to more than a third of a metre in length. Here, rather than retardation in development, there has been an extension of development by a delay in the onset of maturity. This produced a large, robust animal. Its longer life span that produced these morphological features, is associated with a life history strategy like that of the kangaroo rat: small litter size and long gestation period.

Perhaps the most extreme example of the interrelationship between life history strategy and heterochrony is one where there is very little morphological separation between forms, but profound variation in time of maturation. And it has all happened over just the last 200 years in the apple maggot fly, *Rhagoletis pomonella*, which has evolved a number of races that are adapted to feeding from a range of trees (Feder *et al.* 1988; McPherson *et al.* 1988; Smith 1988; Barton *et al.* 1988). Originally adapted to feeding from hawthorn trees in North America this fly has spread to infest trees such as apples, cherries, roses and pears. Behaviourally, offspring of a fly from, say, an apple tree, are more likely to lay their eggs on other apple trees. There are significant differences in the timing of onset of maturity of the fly on different hosts. Under laboratory conditions the "ancestral" hawthorn fly takes between 68 and 75 days to mature. The apple fly takes only 45-49 days. Flies that

infest fruit of the dogwood, however, take between 85 and 93 days. The onset of maturation varies because it is timed to coincide with the period of maturation of the fruit of the host tree (Table 1). The result of this has been not only the establishment of behavioural barriers to gene flow but also developmental barriers, as mating time of the flies from different hosts will vary.

Table 1

Variations in timing of onset of maturity and its relationship to time of fruit maturation in races of the apple maggot fly *Rhagoletis pomonella*. Data from Feder *et al.* (1988), McPherson *et al.* (1988) and Smith (1988)

Host	Days to Maturity	Fruit Maturation Time
Hawthorn trees	68-75	early autumn
Apple trees	45-49	mid-late summer
Dogwood trees	85-93	mid-late autumn

Heterochrony and predation pressure

While heterochrony provides the fuel for evolution, what actually drives evolution along? Why are particular shapes and size evolved and not others? One important aspect that is emerging from this work is the realisation that many evolutionary trends, such as the evolution of horses, are constrained by developmental changes. But why do the trends go in the direction that they do. What is driving them along? The fossil record is replete with examples of such evolutionary trends (McNamara 1988, 1990a), and some are providing indications that predation pressure is a potent force in selecting for particular shapes and sizes. Let me briefly demonstrate one example from the fossil record, then two from living animals.

Many of the evolutionary trends in sea urchins that have been documented from the fossil record in southern Australia parallel evolution of the lineages from shallow to deep water environments over a period of about 40 million years (McNamara 1990b). These urchins are a group known as heart urchins, most of which burrow into the sediment. To evolve from living in coarse sands in shallow water to inhabiting fine sands and muds in deep water necessitates the evolution of particular structures. While many of these heart urchins have lost the long sharp spines characteristic of urchins that roam reef platforms, a few possess a small number on their dorsal surface which have been shown to possess a defensive function.

One lineage of the urchin *Lovenia* shows how the number and distribution of dorsal spines varied from the earliest 20 million year old species through another species that lived 15 million years ago, to the last of the lineage that lived about 10 million years ago. The areas of the urchin's shell covered by these spines progressively decreased along the lineage by pedomorphosis (Fig 9) as the urchin evolved into finer sediments deposited in deeper water (McNamara 1989, Fig 7; McNamara 1990b, Fig 9.9). The spines on the ventral surface of *Lovenia*, however, like those in many other heart urchins, are adapted for digging into the sand. These increased in concentration by peramorphosis along the lineage. A greater concentration of such spines would have been a prerequisite for digging in finer sands.

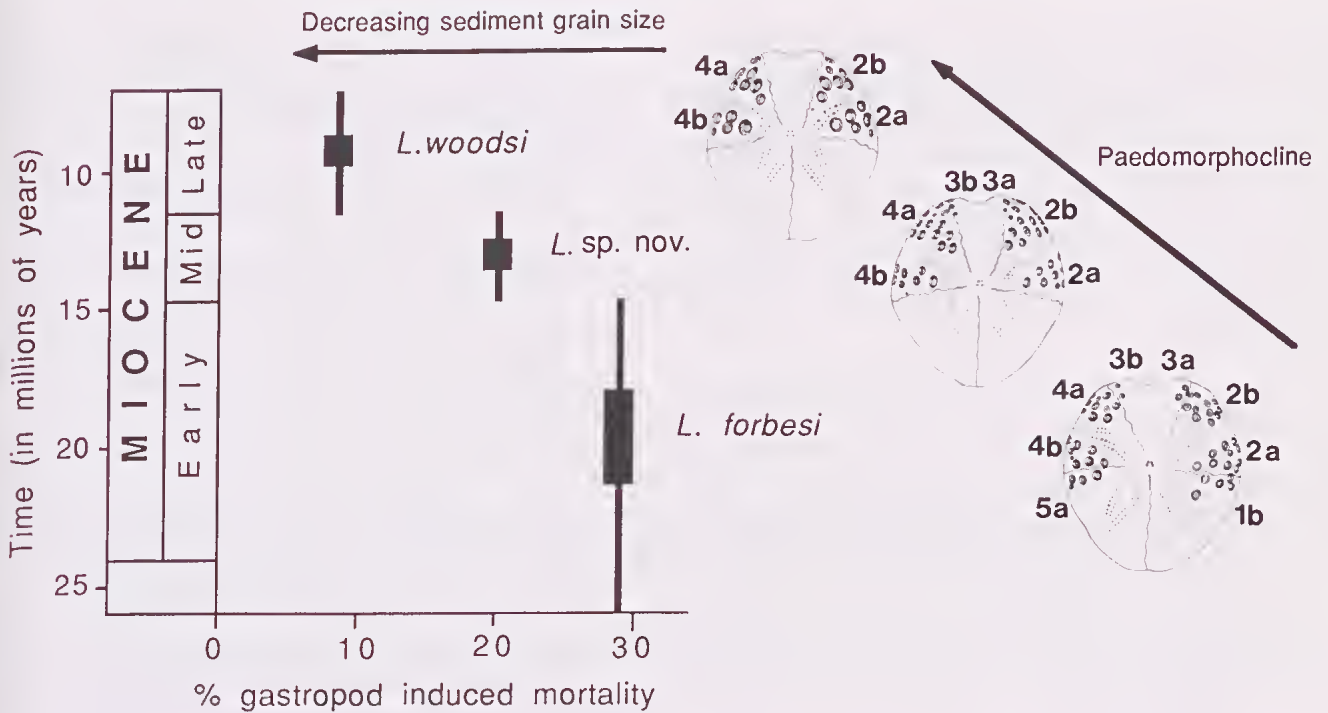


Figure 9. Gastropod induced mortality through time in three Australian species of the heart urchin *Lovenia* showing selection for forms with paedomorphically reduced dorsal spines in regions of lower predation pressure. Reproduced, with permission, from McNamara (1990b).

Many of the urchin fossils bear a small hole in their test, rather like a small bullet hole. These holes were cut by predatory cassid gastropods. By analysing the frequency of occurrence of lethal predation it can be shown that gastropod-induced mortality was nearly 30% in the shallowest water species, that lived in the Early Miocene; 20% in the deeper water intermediate Middle Miocene species, and only 8% in the deepest water species, the last in the lineage that occurred in the Late Miocene (Fig 9). Cassid gastropods are known today to occur with highest frequency in shallow water, and decrease in diversity into deeper water. I would suggest that the high level of predation on these urchins in shallow water was the driving force that directed their evolution, by selection of forms with particular developmental rates, that were better adapted to living in deeper water, where there were fewer predators.

A similar effect can be demonstrated in some living animals. For instance the three-spined stickleback fish *Gasterosteus* shows paedomorphic pelvic reduction that is induced directly by predation pressure (Bell 1988). During development, the pelvic girdle grows to become a prominent spine in forms that live in the sea. In this environment the main predators are other fishes that try to swallow the stickleback whole. A stout spinose pelvic girdle is an effective deterrent to such predators. However, in freshwater habitats there is a shift in the type of predator away from fish to insects. Whereas the pelvic spines are useful armour against other fish they are maladaptive in freshwater because predatory insects use them to grip onto the small fish. Selection pressure in the freshwater environment favours those sticklebacks that reduced the amount of growth of the pelvic spine. There is evidence from the fossil record that such pelvic reduction in sticklebacks is heritable. In a 110,000 year sequence in Miocene rocks pelvic reduction is observed to have occurred (Bell 1988). With the reduction in pelvic spines there was a reduction and then ultimate disappearance of all other fishes from the sequence, indicating that vertebrate predators had gone, replaced, perhaps by invertebrate predators.

Recent work on the freshwater snail *Physella virgata* (Crowl & Covich 1990) has shown that timing of growth and thus shell size can be directly influenced by the presence or absence of predatory crayfish. Populations free from the predator show rapid growth until a shell length of about 4mm, at which time reproduction begins and growth rate declines. The snails live for 3 to 5 months. Introduce a predator into the system in the form of a crayfish and the snails delay their onset of maturity, and so achieve a larger size. As a consequence, individuals live longer. As the crayfish prey preferentially on small snails it is to the snail's advantage to grow to a larger size as rapidly as possible. This switch in the timing of maturation in the snail is caused by a chemical cue introduced by the crayfish.

Conclusions

This brief tour through elements of the animal and plant kingdoms has illustrated the importance of variations to the timing and rate of development in evolution. It is fitting to conclude this address with a final species—*Homo sapiens*. If heterochrony has been so influential in the evolution of so many animals and plants, then there is no reason why it should not also have played an important role in human evolution. Just think of any illustrations in textbooks of hominid evolution: they are invariably portrayed purely in terms of the evolution of adults. But I believe that the whole of the period of development must be investigated to understand fully how humans evolved.

The Dutch anatomist Loius Bolk observed (Bolk 1926) that adult humans possess many features present in juvenile apes, such as flat faces, reduced body hair, relatively large brains housed in thin skull bones, absence of brow ridges and a cranial crest and small teeth that erupt later in life. While there may be a few people you know who resemble adult apes, I'm sure that most would more closely resemble the juvenile (see Gould 1977, Fig 61). However recent work, particularly by Shea (1988) and

McKinney & McNamara (1991), suggests that some of these apparent paedomorphic characters might be overshadowing other developmental changes that have occurred in hominid evolution. There are a number of important characters possessed by adult humans that do not occur in juvenile apes. For example the structure of the base of the skull, which allows us to walk upright and face forward, bears no resemblance to that of a juvenile ape. But most significant is our overall size and our large brain. These are not the product of retarded development. On the contrary they are the product of peramorphosis resulting from our delayed onset of maturity (hypermorphosis), compared with other apes.

We are the late finishers among the primates in terms of our period of extended juvenile growth. Our prolonged period as juveniles has resulted not only in us attaining a larger body size than our ancestors, but also, importantly, a larger brain. Significantly this allowed a longer period in the critical phase of learning. Certainly, like the delphinium flower, we are the product of dissociated heterochrony: some parts of our anatomies are retarded, while others have developed beyond those of our ancestors. But arguably it is these hypermorphic, prolonged features that were the ones that led to the success of our species on this planet, and all that that has entailed.

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